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THE BLACK-AND-TAN RABBIT AND THE SIGNIFICANCE OF MULTIPLE ALLELOMORPHS

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It is well known that the European rabbit has undergone great variation, and now exists in a large number of domesticated varieties. Darwin and most other naturalists speak of this as "variation under domestication," implying that domestication has caused the variation. Modern genetic research, however, indicates that domestication has occasioned the preservation rather than the origin of the fundamental variations involved. But to what extent man through selection is able to modify the fundamental variations which nature occasionally produces as sports is still an open question. Evidence is nevertheless accumulating that certain of these fundamental variations may occur in two or more alternative forms, and the question then arises (1) whether these alternative forms have arisen independently by distinct acts of mutation, or (2) whether one has arisen from another by a process of secondary mutation, or (3) whether one may not have been transmuted into another by a more or less gradual process. Toward the testing of these several hypotheses much genetic research is now being directed. The first step to be taken is evidently to ascertain in how many alternative forms the same fundamental variation may occur and how these forms are interrelated. A further step will be the attempt to produce new alternative forms at will. It is our purpose, in this paper, to discuss a newly discovered alternative form (allelomorph) of the gray, or agouti, type of coat found in wild rabbits. It occurs in the variety known as black-and-tan.

This variety appears to have arisen from the wild gray, or agouti, type without the loss of any known genetic factor, but by a modification in one. Simple loss of genetic factors is believed by most students of genetics to have given rise to black, chocolate and albino varieties of rabbits and other rodents, but a hypothesis of this sort will not fit the present case. No factorial loss can be detected, but only a change in that genetic factor which has been called the *agouti* or gray factor. Under the influence of this factor, what would otherwise be a black variety becomes gray, and what would otherwise be sooty yellow (''tortoise'' of the fanciers) becomes clear yellow (''fawn'' of the fanciers). This same factor converts chocolate into cinnamon (Punnett, 1912). In every way, accordingly, its influence on the coloration of rabbits is similar to that of the agouti factor in guinea-pigs and mice.

But in mice Cuénot (1909) showed that the agouti factor may assume three distinct forms allelomorphic to each other, the effects of which are seen respectively in gray, light-bellied gray, and in yellow mice. Entire absence of agouti marking from the fur (non-agouti) forms a fourth allelomorph in the series.

In guinea-pigs the agouti factor assumes two alternative conditions, the effects of which are seen in ordinary (light-bellied) agoutis and in agoutis with ''ticked'' bellies, respectively (Detlefsen, 1914). These two conditions correspond closely in appearance and in order of dominance to the light-bellied gray and the ordinary gray of mice, the former being dominant in both cases. Non-agouti is an allelomorph to both, as in mice.

The peculiarity of the agouti seen in black-and-tan rabbits is that it produces less extensive ticking of the fur than does ordinary agouti. In a typical black-and-tan rabbit the light-colored (yellowish) bands on the hairs, which constitute the ''ticking,'' occur only sparingly on the sides of the body, and not at all on the back or the head. But the under side of the body, including the throat and under surface of the tail, are light (yellowish or whitish) and the back of the neck and inside of the ears bear reddish or yellowish pigment, as in gray rabbits. The typical black-and-tan rabbit of the fanciers has very intense pigmentation which deepens the shade of the ''tan'' (yellow) found on belly, sides, etc. But this intensity is inherited independently of the agouti factor as crosses with dilute colored varieties of rabbit show. For a cross between black-and-tan and blue produces in F_2 (1) *blue-and-tans* as well as (2) black-and-tans, (3) blacks, and (4) blues. This result is strictly parallel with that obtained by crossing intense gray rabbits with blue ones. In that case there are produced (1) blue gray, (2) intense gray, (3) black, and (4) blue young in F_2. It is evident that in each case a dihybrid cross is made and that the end products are the same in the two series except for the difference in the agouti marking of varieties (1) and (2). The natural conclusion is that black-and-tan contains an alternative form of agouti to that found in gray rabbits. If so, it should be capable everywhere of substitution for gray, wherever the latter occurs throughout the entire series of color varieties, and indeed this appears to be the case.

That the black-and-tan factor, like the ordinary agouti factor, is independent of the extension-restriction pair of allelomorphs is shown by a cross of black-and-tan with sooty yellow (*i. e.*, non-agouti yellow or "tortoise"). F_2 contains (1) black-and-tan, (2) black, (3) yellow ("fawn"), and (4) sooty yellow ("tortoise") young. The first two are varieties with extended pigmentation, and the second two are varieties with *restricted* pigmentation; further, varieties (1) and (3) contain *modified* agouti, but varieties (2) and (4) do not.

If a gray rabbit had been used, instead of a black-and-tan, in making the cross just described, three of the four varieties obtained in F_2 would have been indistinguishable from those enumerated, and the fourth one would merely have been gray instead of black-and-tan. This supports the view that black-and-tan is merely an alternative form of gray.

Further, we have evidence to show that the black-and-tan form of agouti, like the agouti of gray rabbits, is independent of the genetic factors which respectively produce Dutch pattern, English pattern, and angora coat, since we have been able to produce individuals in which black-and-tan was associated with each one of these Mendelizing characters, as well as others in which it was not associated with them. Finally Haecker (1912) has shown that black-and-tan, like the ordinary form of agouti, is independent of albinism, since when black-and-tans are crossed with Himalayan albinos, not only these two varieties are obtained in the F_2 generation, but also *blacks*. The proportions in which these three varieties were obtained by Haecker approximate the modified dihybrid ratio, 9 black-and-tan: 3 black: 4 Himalayan. One of the two Mendelian pairs concerned is color *vs.* albinism; the other and independent one, black-and-tan *vs.* black.

It is known that if a gray rabbit is used, instead of a black-and-tan one, in a cross with Himalayan albinos, the same 9:3:4 ratio is obtained in F_2, of grays, blacks, and albinos, respectively. The observed results differ, in the two cases, only in the substitution of gray for black-and-tan, which is further evidence that it is only another form of the same genetic factor.

Notwithstanding all this consistent and converging evidence, it is possible that the modified form of agouti seen in black-and-tan is not due to a changed agouti factor itself, but to the modifying action of a factor associated with it which partially inhibits its action. Here we must consider two subordinate possibilities: (*a*) that the supposed modifier is wholly independent of the agouti factor, and (*b*) that it is coupled with the agouti factor. The first possibility is readily disproved; the second one is not so easily disposed of.

(*a*) If black-and-tan were due to the action of an independent modifying factor associated with agouti, a cross of black-and-tan with ordinary black should permit the separation of agouti from its supposed modifier in a considerable part of the F_1 gametes and F_2 zygotes, so that we should expect F_2 to contain gray animals as well as blacks and black-and-tans. But experiments started several years ago at the Bussey Institution show that when black is crossed with black-and-tan no gray offspring are obtained either in F_1 or in F_2, but only black-and-tans in

F_1, and black-and-tans and blacks in F_2. This result shows that black-and-tan is a simple dominant over black.

To establish the allelomorphism of black-and-tan with gray the following experiments may be cited. A black-and-tan rabbit heterozygous for black was crossed with a pure-bred Belgian hare, which variety possesses the genetic color factors of wild rabbits, including the ordinary agouti factor. All the F_1 young were gray, closely resembling Belgian hares, but proved to be genetically of two types. For, when mated with black rabbits, some of them produced gray young and black young, while others (even when mated, as in some cases, with the same black animals) produced gray young and black-and-tan young. This result was quite what was to be expected if gray, black-and-tan and black are mutually allelomorphic conditions. On no other hypothesis which we can suggest was it to be expected. For the black-and-tan parent in the cross was known to be heterozygous for black. It accordingly should form two sorts of gametes, black and black-and-tan respectively, provided that these conditions are allelomorphic to each other. The Belgian hare parent was known to transmit gray in all its gametes. The combinations expected from the cross are therefore of two types, viz.: (1) gray combined with black, and (2) gray combined with black-and-tan. It is well known that gray and black are allelomorphs of each other, the former being dominant. Zygotes of type (1), therefore, should produce gametes of two sorts, gray and black; and when back-crossed with black should produce equal numbers of gray young and black ones but no black-and-tan young. We have tested 12 F_1 gray young from this cross (6 males and 6 females) which are evidently of type (1). Mated with black animals, they have produced 69 gray young, and 65 black ones, but no black-and-tans.

On the other hand 8 F_1 gray rabbits from the cross under discussion have proved to be of type (2), producing gray young and black-and-tan young but no black ones. Together they have produced 44 gray and 51 black-and-tan young, besides 14 other young (two litters) which were certainly not blacks, since they had light bellies, but which died before attaining the age at which gray can be distinguished from black-and-tan. It is certain that among the 109 young produced by the 8 animals of type (2) not a single one was black.

But if black-and-tan is not an actual allelomorph of gray, black young as well as black-and-tans should have been produced in the foregoing case. For if black-and-tan is not allelomorphic with gray, or is due to an independent inhibitor of gray, then an F_1 gray should produce gametes of *four* sorts, rather than as indicated of *two* sorts; *i. e.*, gametes should arise which transmit *both* gray and black-and-tan, and others which transmit *neither* gray nor black-and-tan. The former sort possibly might not be capable of immediate detection in the back-cross with black, but the latter should be readily discovered since they would necessarily produce black young (neither gray nor black-and-tan). The total absence of black young from the litters produced by type (2) matings therefore indicates strongly that gray and black-and-tan are allelomorphs of each other.

(*b*) An alternative view, however, deserves consideration. If gray and black-and-tan are not actual allelomorphs, it is conceivable that they may each be closely "coupled" with a common structure in the germ cells and so *behave* as allelomorphs under ordinary circumstances, though not being such in reality. Or, what would give the same practical result, gray and black-and-tan might be supposed to contain the same agouti factor, but this might be considered in one as closely coupled with a modifying factor which made its action different. Neither form of this hypothesis is capable of proof or disproof, for which reason alone the hypothesis is unimportant, but its probability grows less the larger the number of records obtained which show no breaking of the supposed coupling. Our cases are not as yet numerous enough to throw much light on this question, but so many cases have already been discovered in which characters assume three or more mutually allelomorphic conditions and in which no evidence of coupled modifiers has yet been discovered, that the existence of such assumed modifiers seems at present doubtful.

Besides the triple or quadruple series of agouti allelomorphs now known for mice, guinea-pigs and rabbits, at least three other Mendelian factors concerned in the pigmentation of rodents vary discontinuously in this way.

1. Castle (1905) and Punnett (1912) have shown that the Himalayan rabbit possesses a form of albinism allelomorphic with that of ordinary albino rabbits, and that both are allelomorphic to ordinary pigmentation. Guinea-pigs show an even more extended series of albino allelomorphs (Castle, 1914, Wright, unpublished data).

2. Punnett (1912) has discovered in rabbits an alternative form of the "extension" factor, one in the presence of which the agouti factor produces a less amount of ticking than normally. He describes it as a *darkened* extension, *i. e.,* as ordinary extension modified by a coupled darkening factor. This is of course only an alternative form of statement to saying that extension occurs in two forms, for he discovered no cases in which the hypothetical coupling was broken. The three allelomorphs in the case of Punnett's rabbits were accordingly: 1, *ordinary extension;* 2, *darkened extension,* and 3, *restriction.*

3. In still another Mendelian factor affecting the pigmentation of rodents discontinuous variation occurs attended almost certainly by the formation of a series of allelomorphs. Cuénot (1904) stated that white-spotting in mice occurs in a graded series of conditions as regards the amount or extent of the white areas. He found that widely separated stages in the series Mendelize on crossing, *i. e.,* that the segregates fluctuate about modal conditions corresponding roughly with the conditions of spotting found in the respective parents crossed, and he concluded the number of allelomorphs which it would be possible to find in the series to be indefinitely great. Subsequent studies of the subject made by Little (1914) in mice, and by Castle and Phillips (1914) in rats, have not served to simplify the matter, and yet they confirm Cué-

not's general idea that a series of mutually allelomorphic conditions of spotting exists. Unquestionably in rats, "hooded" and "Irish" are such modal conditions of spotting, allelomorphic with each other and with the unspotted or self condition (Doncaster, 1905; MacCurdy and Castle, 1907; Castle and Phillips, 1914). The last-named authors find that independent factorial modifiers probably affect the extent of the spotting and yet that, aside from such modifiers, the spotting factor proper may assume relatively stable allelomorphic conditions which Mendelize when crosses are made between stages sufficiently distinct. The point of especial interest in allelomorphic conditions of spotting is that they are *not* perfectly stable, but are capable of gradual and apparently indefinite modification through the selection of fluctuations either plus or minus. It would be premature to conclude that similar fluctuations (though perhaps less conspicuous ones) do not occur about the modal conditions of other genetic factors which show allelomorphic variation. The black-and-tan form of agouti certainly fluctuates in the amount of ticking found on the sides of the body and the head; doubtless some of this fluctuation may be due to factors genetically distinct from the chief allelomorphic factor concerned, but there is at present no sufficient ground for supposing the chief factor itself to be incapable of fluctuation. Indeed, it seems highly probable, in the light of evidence already obtained, that the present modal condition of the black-and-tan character is one which has been attained only as a result of persistent selection, and that reversed selection will carry it back appreciably nearer to the modal condition seen in gray rabbits. Accordingly, it appears doubtful whether allelomorphs are themselves perfectly and permanently stable. Moreover, the rapid increase of recognized allelomorphs makes us wonder whether their number is limited and definite. Black-and-tan represents, on the whole, an intermediate condition between black and gray. Is it not conceivable that intermediates may yet be discovered between black-and-tan and black, or between black-and-tan and gray, or even that black-and-tan itself might be displaced to such an intermediate condition by selection of its fluctuations? Here are fruitful fields of inquiry to be cultivated before we conclude with the exponents of "exact" heredity that selection of fluctuations is useless and that only mutations count in evolution.

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